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# BIOLOGICAL BULLETIN

## MORPHOLOGY AND ORIENTATION OF THE OTOCYSTS OF GONIONEMUS.[1]

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### INTRODUCTION.

*Gonionemus* is used as an example of the *Hydro-medusæ* in many zoölogical laboratories of this country. In spite of this fact relatively little is known regarding the morphology and orientation of the sense organs of the representatives of this genus. Both the location and the structure of the otocysts have been very imperfectly treated in the literature. Frequently morphological and experimental treatises mentioning the otocysts refer the reader to the works upon other genera, the otocysts of which are presumed to be essentially similar to those of *Gonionemus*. In studying specimens of *Gonionemus vertens* Ag. and of *G. murbachii* Mayer the writer was impressed by the lack of agreement between his direct observations and the published statements by various early workers. These discrepancies led the writer to investigate the problem further in an attempt to discover the source of the statements which have been so generally incorporated into the literature and to determine, if possible, the precise structure and relationships of the otocysts in this genus.

On the Pacific coast of this country *G. vertens* A. Ag. occurs in the Puget Sound region and on the Atlantic coast *G. murbachii* Mayer is found in abundance in the Eel Pond at Woods Hole, Mass. Many references in the older literature incorrectly refer to the Atlantic species as *G. vertens* because at that time the Atlantic form was not considered as specifically distinct from the

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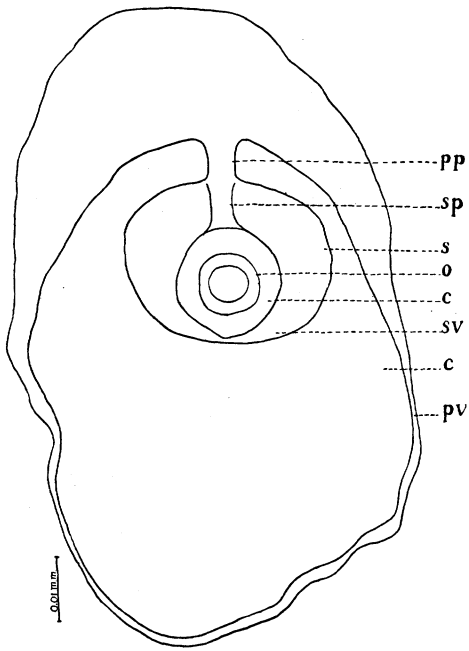
type of the genus. In 1895 Murbach mentioned certain differences between the two forms and in consideration for his work upon the Atlantic species A. G. Mayer (1901) described it as a distinct species under the name of *Gonionemus murbachii*.

The terms otocyst, statocyst, and lithocyst have been used interchangeably throughout the literature on Cœlenterates. In this paper the term otocyst is used in referring to the entire structure which is supposed to function as an organ of equilibrium. A careful study of the otocysts in *Gonionemus* has revealed the fact that the terminology ordinarily employed in describing the otocyst is entirely inadequate for an intelligible description of the parts and understanding of their functional relations. In *Gonionemus* the otocyst is not a simple vesicle enclosing an otolith as has usually been considered the case. From a morphological point of view there is considerable evidence that in *Gonionemus* the large vesicular structure is merely an adaptation for the protection of the true sensory apparatus all of which is lodged within the structure that has ordinarily been termed the otolith. This obvious confusion of terms renders a detailed description of the organ necessary.

Details of the organization of the otocyst are shown in Text Figure 1. The wall of the primary vesicle (*pv*) is the outermost wall of the entire organ and encloses a fluid-filled cavity (*c*) within which the spheroid (*s*) is suspended by the primary pedicel (*pp*). The thick wall of the spheroid encloses the fluid-filled cavity which is designated as the secondary vesicle (*sv*). Within the secondary vesicle rests the otolith (*o*), free to move about within the fluid-filled chamber. Extending from the distal end of the primary pedicel to the membranous lining of the secondary vesicle is a distinctly differentiated region to which the term secondary pedicel (*sp*) has been applied.

This investigation was carried on under the general direction of Dr. H. J. Van Cleave, to whom the writer is greatly indebted for suggestions and for securing the material and the identification of the species under consideration. Individuals of *Gonionemus murbachii* were obtained through the Supply Department of the Woods Hole Marine Biological Station for comparison

with those of *G. vertens* upon which the greater part of the work was done. Specimens of *G. vertens* collected at Friday Harbor, Washington, were submitted to Dr. Alfred G. Mayer and to Dr.




TEXT FIGURE 1. General organization of the otocyst of *Gonionemus: p v,* primary vesicle; *c,* fluid filled cavity; *s,* spheroid; *p p,* primary pedicel; *s v,* secondary vesicle; *o,* otolith; *s p,* secondary pedicel.

Henry B. Bigelow, both of whom very kindly verified the tentative identification of the species.

While the present paper deals primarily with the finer structure of the otocyst the latter part is devoted to a discussion of the orientation of the otocyst in the organism.

## METHODS OF STUDY.

Specimens preserved in formalin were too opaque for accurate observations of the otocysts. Serial sections and toto-mounts of the bell margin, including ring canal, otocysts, and tentacles were prepared for the detailed study of the morphology and the orientation of the otocysts. The toto-mounts were made by

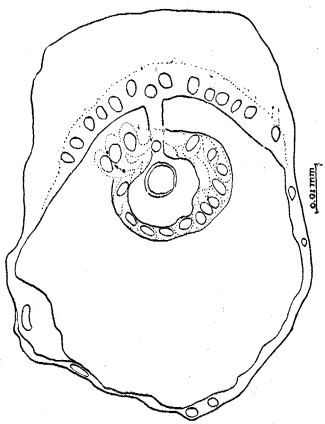
trimming the tentacles close to the bell margin with fine scissors and then clipping this rim, with the velum included, free from the remainder of the bell. Such preparations were stained with borax carmine and mounted in damar. The otocysts, though embedded in the mesoglea, were by this method sharply defined and readily visible for accurate observations. In some specimens prepared in this manner the finer details of structure could be determined. By careful manipulation, mounts prepared in this manner showed practically no distortion. Individuals 9 to 15 mm. in diameter were dehydrated, cleared, and mounted in damar with a shrinkage of 1 mm. or less in diameter. This shrinkage was obviously sustained uniformly by the various tissues for no evidences of wrinkling or distortion of parts were observable in the finished preparations. All drawings were made with the camera lucida from prepared mounts and sections.

## Structure of the Otocyst.

Murbach (1903: 205) dismisses the anatomy of the otocysts in *Gonionemus* with the footnote: "The finer anatomy is naturally omitted. The description of the nervous system and the otocyst given in 'Das Nervensystem und die Sinnesorgane der Medusen,' O. u. R. Hertwig, text, pp. 48–69, Plates 4 and 5, fits very nearly those of *Gonionemus*." A careful examination of the Hertwig descriptions and drawings of otocysts in other genera reveals many points where a closer "fit" might be desired if the descriptions and drawings are to cover the conditions found in *Gonionemus*.

Superficial examination under a compound microscope reveals the otocysts of *Gonionemus* as tiny bubbles, each of which usually encloses a single spherical object. This last mentioned body has usually been considered as the otolith, though it probably comprises the entire sensory mechanism of the organ as indicated in the introduction to this paper. Detailed structure of this body is shown in Fig. 2, Plate I., which was drawn from a 15 $\mu$ section. This figure shows only the spheroid pendant from the wall of the primary vesicle by the minute primary pedicel (*pp*). The heavily nucleated cells which comprise the wall of the secondary

vesicle (*sv*) completely envelope the secondary pedicel (*sp*). The true otolith (*o*) is shown within the secondary vesicle. In the section from which this drawing was made a small tangential slice such as is shown in Fig. 3, Plate I., had been cut from the surface of the spheriod thus disclosing the cavity of the secondary vesicle. No sensory hairs or ridges were demonstrated. Perkins (1902: 786) also calls attention to the absence of such structures, though his observations were probably confined to the walls of the primary vesicle. In sections a thin tangential slice from the surface of the spheroid, Text Figure 2, may at



TEXT FIGURE 2. Tangential slice only partly removed from wall of spheroid.

first glance remind one of the projections figured by Hertwig (1879: 183, Figs. 1 and 2) for *Carmarina*.

The primary pedicel measures 0.043 mm. in diameter and 0.069 mm. in length. At its proximal end a single large nucleus is found. This pedicel is very delicate for in sectioning, it, together with the spheroid, is often torn loose from the cyst wall. In other cases only the spheroid is torn away from the distal end of the pedicel and may be found elsewhere on the slide. Goto (1903: 8) records encountering the same difficulty in the preparation of sections.

The secondary pedicel measures 0.115 mm. in length. Its diameter near the middle is about 0.023 mm. but the distal end is

expanded to about 0.043 mm. Two nuclei of apparently fixed relationships are found in the secondary pedicel, one near the proximal and the other near the distal end.

The cavity of the secondary vesicle is normally spherical in form though it is capable of some distortion. The diameter is about 0.138 mm. The contents of this cavity take stains so lightly and so evenly that there is strong evidence that only a fluid is present. Two or three concentric rings are observable in the spherical otolith contained within the secondary vesicle (Figs. 4–5, Plate I.). There is considerable variability in the size of the otolith. Some of the largest measured 0.069 mm. in diameter. The fluid in which the specimens were preserved was distinctly acid, consequently any calcareous deposits that might have been present in the otolith had been destroyed, leaving only the supporting structures. Perkins (1902: 786) refers to the otolith as "a calcium salt deposit in an organic matrix." In the specimens examined the otolith had no fixed position within the secondary vesicle but was apparently free to move about in the fluid filled space. The entire sensory mechanism as ordinarily described for an otocyst is thus contained within the confines of the spheroid. In the light of this morphological evidence it might be easily possible that the destruction of the primary vesicle need not appreciably impair the functioning of the organ.

Murbach (1903: 206) in experiments upon the function of the otocysts of *Gonionemus* collapsed the "otocysts" by thrusting them with a fine needle. In all probability the injury inflicted did not extend beyond the collapsing of the primary vesicle. According to his statements the specimens continued to act normally after this treatment. Upon the results of these experiments and upon the behavior of a single individual from which the otocysts were excised he based his conclusion that the otocysts play no important part in establishing the equilibrium in *Gonionemus*. The more or less normal behavior of the much mutilated individual from which the otocysts were cut is not readily explainable. On the other hand, in view of the fact that morphologically the entire sensory mechanism of the otocyst seems to be confined to the secondary vesicle there is little reason to expect serious

interference with the functioning of that organ when only the protective primary vesicle is collapsed.

My observations upon specimens of *G. vertens* and of *G. murbachii* have failed to disclose any essential difference in the details of structure or in the general orientation of the otocysts of these two species.

## Relations of Otocysts to Bell Margin.

Because of the reliance placed upon the works of previous investigators and writers on the subject, Mayer's "Medusæ of the World" includes several erroneous statements and incorrect figures of the otocysts of *Gonionemus*. Few authors, with the exception of Mayer, have attempted to describe definitely the location of the otocysts with reference to their position on the margin of the bell. It seems probable that his description is based chiefly on Perkins' publication (1903: 786) which has been extensively quoted by Mayer though his observations upon the otocysts are very misleading. In Plate 34, Fig. 19, Perkins has reproduced a drawing by Professor Brooks which shows the otocysts as external projections from the margin of the bell between the bases of the tentacles. Further, the drawing of the "radial transverse section" of the bell (Fig. 25 of his same plate) confirms the impression of their external location. His explanation of their origin is as follows:

> In the case of the sensory clubs, the endodermal tissue of the circular canal grows down in a plug into the ectodermal tissue of the bell margin. This latter becomes closely applied to the outside of the plug, as a thin investing epithelium, and it also spreads out in a thin lamella over the inner surface of the capsule which appears in the ectoderm of the developing club.

In his summary Perkins (1903: 789) says, "sense organs appear at determinate points on the bell margin." The work in this article on sense organs seems to be principally that of Professor W. K. Brooks whose observations were apparently accepted by Perkins without attempt at verification.

Mayer (1910: 341) in his synopsis of the genus seems to have incorporated the foregoing incorrect observations bodily for he refers to the otocysts as "lithocysts external." On page 342 of the same work he again states that there are "numerous ex-

ternal lithocysts upon the bell margin between the tentacles." In characterizing the genus *Cubaia* (page 351), he states that there are "lithocysts projecting outward as in *Gonionemus*". . . "this genus is closely related to *Vallentinia* Brown 1902 but in *Vallentinia* the lithocysts are enclosed and on the inner side of the margin, whereas in *Cubaia* they are external and on the lower side of the margin between the tentacles." The plates of the same monograph are just as confusing as the foregoing descriptions in the manner in which the otocysts are located. Otocysts are shown as distinct projections from the external margin of the bell in Fig. 1 of Plate 45, though Fig. 2 of the same plate and Fig. 3 of Plate 46 correctly portray them embedded in the mesoglea as outgrowths from the ring canal.

The location of the otocyst within the mesoglea and the orientation with reference to other structures is shown in Fig. 1, Plate I.

## Relations of Otocysts to Tentacles.

Hargitt (1910: 249) referring to the location of the otocysts, says: "Normally they should occur in somewhat symmetrical order between the bases of the tentacles. This, however, is rarely the case." Mayer (1910: 342) gives the number of tentacles for specimens of *G. vertens* 15 mm. in diameter as 60 to 70 but it appears that his count is too low. In the following table are given the data regarding the numbers of otocysts and tentacles in part of the material studied in the present investigation.

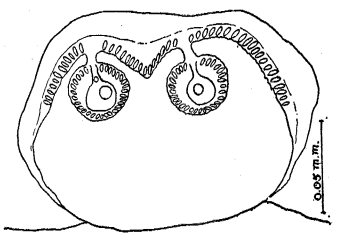
### Table I.

Relative Numbers of Otocysts and Tentacles in Gonionemus.

| Specimen Number. | Diameter of Bell After Clearing. | No. of Tentacles. | No. of Otocysts. |
|---|---|---|---|
| *G. vertens* | | | |
| 1 | 14.5 mm. | 91 | 76 |
| 2 | 14 | 86 | 73 |
| 3 | 14 | 99 | 72 |
| 4 | 12 | 84 | 60 |
| 5 | 11 | 94 | 75 |
| 6 | 11 | 101 | 78 |
| 7 | 10 | 94 | 89 |
| 8 | 9 | 79 | 61 |
| 9 | 9 | 83 | 57 |
| 10 | 8 | 79 | 60 |
| *G. murbachii* | | | |
| 1 | 9 | 48 | 61 |
| 2 | 10 | 64 | 70 |

With reference to the tentacles these organs display no absolutely fixed relationship. Though they usually alternate with the tentacles they may occur in pairs between two adjacent tentacles or two or more tentacles in continuous sequence may have no intervening otocyst.

In *G. vertens,* nos. 6 and 7 had three paired otocysts between adjacent tentacles; no. 7 also had two abnormal otocysts with two




TEXT FIGURE 3. Abnormal otocyst with two sensory spheroids within the same primary vesicle.

sensory spheroids in each capsule Text Figure 3. Hargitt (1901: 249) has noted this last mentioned variation and has called attention to its relative infrequence. Specimen no. 1 of *G. murbachii* had thirteen paired otocysts and no. 2 of the same species had eight.

## SUMMARY.

1. There are two distinct vesicles in the otocyst of *Gonionemus.*

2. It seems probable that the conspicuous primary vesicle has chiefly a protective function, enclosing the essential sensory mechanism.

3. The secondary vesicle contains the otolith within a fluid-filled cavity.

4. No sensory hairs or ridges have been demonstrated.

5. Puncture of the primary vesicle as practiced by Murbach and others probably does not impair the essential sensory mechanism.

6. The otocysts of *G. vertens* and of *G. murbachii* are in close proximity to the periphery of the ring canal, their capsules imbedded in the mesoglea so that no portion of them protrudes beyond the margin of the bell.

7. The number and arrangement of otocysts and tentacles in *Gonionemus* is variable.

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## EXPLANATION OF PLATE.

### SYMBOLS.

*c*, cavity of secondary vesicle,
*e c*, ectoderm,
*e n*, endoderm,
*e x*, exumbrella,
*m*, mesoglea,
*n*, nerve ring,
*n c*, nettling cells,
*o*, otolith,
*p p*, primary pedicel,
*r*, ring canal,
*s*, spheroid,
*s l*, supporting layer,
*s p*, secondary pedicel,
*s u*, subumbrella,
*s v*, secondary vesicle,
*v*, velum.

### PLATE I.

The otocyst of *Gonionemus vertens*. All drawings were made with the camera lucida. The projected scale indicating magnification in each instance has the value of 0.01 mm.

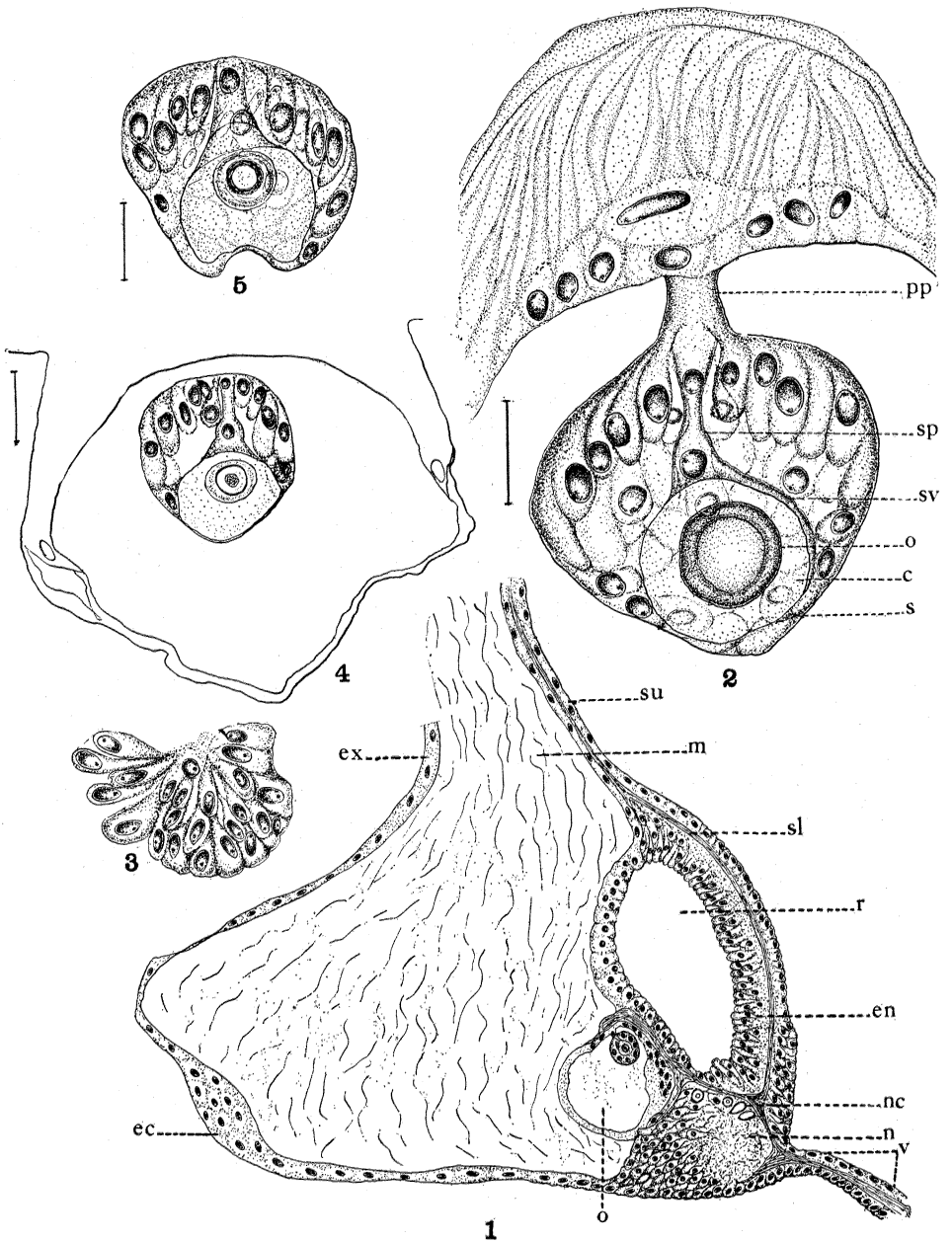
FIG. 1. Section through bell margin showing general location of the otocyst within the mesoglea and its orientation with reference to ring canal.

FIG. 2. Longitudinal section through the spheroid of an otocyst showing histological details.

FIG. 3. Tangential slice from the wall of the spheroid similar to the section removed from the front surface of the wall of the secondary vesicle in the foregoing figure.

FIG. 4. Longitudinal section through an otocyst to show the concentric rings within the otolith.

FIG. 5. A spheroid with a portion of the wall of the secondary vesicle removed.

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